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INTRODUCTION

Drifting oyster larvae often survive by fastening their shells to those of preceding generations, making shell aggregates. Many other permanently sedentary organisms also attach themselves to oyster shells; thus arise oyster shell communities, in which we may find bacteria, diatoms, red, green and brown algae, protozoans, sponges, hydroids, actinians, bryozoa, pelecypods and ascidians as fixed permanent dwellers.

Moreover, these sedentary communities are frequented and made use of in various ways by animals of less sedentary habit, such as annelids, nematodes and platyhelminthes, rotifers, mollusca, acarida, crustacea, and some echinoderms and vertebrates.

Back in 1873 A. E. Verrill (22) named 190 kinds of animals as occurring on oyster beds, and Nelson (19) says: “The shell of an oyster is a veritable zoologist’s paradise, for on it may be found representatives of every phylum of the animal kingdom.”

That the ciliated protozoans, folliculinids, are wide-spread members of this oyster-shell community is to be demonstrated in the present paper.

WHAT ARE FOLLICULINIDS AND WHERE FOUND?

The family Folliculinidae has been separated from the Stentors as more complex in feeding apparatus and as dwelling long in secreted
tests having forms and sizes characteristic of different species and genera. Most of them have been found in the sea.

First seen on the coast of Denmark on algae in 1781, they have been found since on algae, flowering plants, stones, shells, wood, hydroids, bryozoa, serpula tubes and even on the surfaces of certain living crustacea. Various species have been recorded from the Arctic and the Antarctic, the Atlantic and the Pacific, the Indian Ocean, the White Sea, the Baltic, the Mediterranean and the Chesapeake Bay. As yet they are not on record from most of Asia, as well as most all Australia and all the coasts of South America. And there is but one record from Africa and the Pacific coasts of North America (7). Their world-wide distribution may be due in part to their habit of attaching themselves to solid objects, some of which float and may be carried by currents, and in part to their habit of escaping from their tests to swim free when they may be borne by currents. However, their occurrence in fresh waters in Switzerland, France, England and Uruguay needs some different explanation. May the adults survive on the feet of aquatic birds or in the hair of water-frequenting mammals? At present we have no knowledge of spores of folliculinids that might be carried by winds.

ADVANTAGES OF USING OYSTER SHELLS TO EXTEND KNOWN FACTS AS TO GEOGRAPHICAL DISTRIBUTION

Since folliculinids are taken in brackish as well as in more saline waters and since they are attached to various sorts of mollusc shells, it was to be expected that they would be found on oyster shells; and there is one mention of their being found in Europe on oyster shells together with other shells. That they may abound on oyster shells was put on record in 1880 by Ryder (20) when stationed with the U. S. Fish Commission steamer, Fish Hawk, at St. Jerome, St. Mary’s County, Maryland. Forty-two and forty-three years later we found stones and oyster shells in parts of that same harbor thick set with two kinds of folliculinids.

As oysters are readily recognized and marketed, it seemed that an examination of oyster shells from various localities should be useful in extending the known geographical distribution of folliculinids in American waters, where they are little known.

Many zoologists in the United States and Canada were so kind as to send me random collections of oyster shells from the most northerly known beds in the Gulf of St. Lawrence, Prince Edward Island and Nova Scotia, down along the Atlantic shores of Maine, Massachusetts, New York, New Jersey, Maryland, Virginia, North Carolina, Florida,
Louisiana and Texas, as well as from the Pacific shores of California; in all these localities folliculinids were found on oyster shells.

**TAXONOMY**

In Europe folliculinids have been described as different species and genera, and here in America several of these different sorts have been recognized. Following the classification of Dons (12), rather than that of Kahl (16), but with consideration of the views of Fremiet (13), and of Hadzi (15), we here "lump" many diversities to reduce the forms in North America to the following ten: of the Eufolliculininae, we recognize here a form that seems like Mueller's (18) *Folliculina ampulla*, another that Hadzi (15) has described as *Metafolliculina andrewsi*, as well as the two new commensals, *Pseudoparafolliculina portitor* (6) and *Brachyfolliculina paguri* (3), and at Woods Hole Martin Burkenroad found what is probably the *Metafolliculina longicollis* of Hadzi (15); of the Semifolliculininae, we recognize *Lagotia viridis* (9), *L. simplex* Dons (12), *Parafolliculina violacea* (Giard) (4), *Parafolliculina amphora* Dons (2). In addition, Dons (10) in 1915 stated that his *Lagotia (semifolliculina) spirorbis* occurred on the eastern coast of North America.

Of these, *Folliculina ampulla* Mueller has not been reported previously from America; the peculiar tests found on oyster shells are near to Dons' figure and interpretations of than little-known and often erroneously identified species, but more study of the living animals is much needed. The second form, *Metafolliculina andrewsi*, has local differences in size and grouping of tests that may warrant separation from the form recognized by Hadzi. The third is an undescribed commensal of Limulus to be named *Pseudoparafolliculina portitor*. The fourth is a commensal of hermit crabs from Maine called *Brachyfolliculina paguri*, Andrews and Reinhard (3). The fifth, *Lagotia viridis*, includes the numerous synonyms recognized by Dons and may yet be subdivided. The sixth, *Lagotia simplex*, was found at Woods Hole, Massachusetts by Fremiet and more recently (7) on hermit crabs from California. The seventh, *Parafolliculina violacea*, everywhere agrees well with European forms as well as those mentioned from Woods Hole and from Beaufort by the present writer, but there is a marked variety with stalk in Long Island Sound. The eighth, *Parafolliculina amphora*, is everywhere in agreement with those described (2) from near Baltimore, Md. The ninth, *Lagotia spirorbis* has not yet been found again in America. The tenth, *Metafolliculina longicollis* Hadzi, though like the form from the French coast called *Folliculinopsis producta* Wright 1859 by Fremiet needs more study and may prove to be a variety of *M. andrewsi*. 
GENERAL CONSIDERATIONS

While oyster shells serve to reveal the existence of these protozoans all along the Atlantic coasts of North America, there may be some doubt as to whether all the habitats were original, natural, or perhaps only recently acquired by aid of man. That is, oysters are carried from place to place to be planted and transplanted; from Connecticut to Long Island, and from more southern waters to more northern. However, it is not known if folliculinids can remain alive in these transports of oysters. Additions to the native fauna may also occur when folliculinids attach themselves to boats that pass from one body of water to another.

Previously folliculinids had been recorded only from the regions of Newport, R. I., Woods Hole, Mass., branches of the Chesapeake in Maryland, and Beaufort, North Carolina, but the examination of oyster shells has served to greatly extend the known distribution. In fact, we find that of the forty-five actual places in which folliculinids have been found on this continent, twenty-two are occurrences only on oyster shells, five on oyster shells and other objects, and of the remaining eighteen, some dozen, that is two-thirds, were merely subdivisions of the general occurrence on submerged flowering plants along the shores of side branches of the Chesapeake, near Baltimore, Md. Considering these as one locality, we find that of thirty-three different localities twenty-seven were places where the folliculinids occurred on oyster shells.

The number of shells taken at random from each of the 27 localities ran from 2-75, and of them a very variable percentage bore folliculinids; in three or four instances this was 100 percent; it was 50 percent or greater in seven instances; and it was lower in the rest. The entire number of shells examined was 600, and of these 200 bore folliculinids, that is, 33 per cent.

Some shells, in most all localities tested, bore folliculinids, but the following were samples taken that bore no folliculinids: a dozen shells from the upper part of the harbor at Woods Hole, Mass., June, 1942; shells bought as from the Patuxent R., Md., Jan. 1942; 18 shells off Sherwood Forest, West Round Bay, Md., July 28, 1943; shells from off Sandy Point, near Annapolis, Md., autumn, 1941; five shells from the Eliot River near Charlottetown, Prince Edward Is., Canada, Sept. 14, 1942; and eight shells from Frederick Cove, Conway Narrows oyster area, P. E. Is., Sept. 14, 1942.

Obviously, we cannot infer that folliculinids are absent from these localities until much more extensive samples are studied, for the distribution of folliculinids over an oyster area is probably similar to
that over the flowering aquatics along the shores of the Severn River branch of the Chesapeake Bay, where some patches of weeds were thickly populated and adjacent areas devoid of folliculinids.

The number of folliculinids found on one oyster shell ranged from one to several hundred.

It may be emphasized that inasmuch as part of the oyster shell is in contact with the bottom or with other shells and may be partly overgrown with organisms to which the folliculinids do not attach, the remaining areas of shells capable of bearing folliculinids may be small. Over such favorable areas the folliculinids often are scattered at random, but often they are aggregated in depressions or in protected regions of the shell surface, or within an empty shell.

The individuals may stand isolated, far apart, or may be grouped as in flocks with various densities from \( \frac{1}{8} \) individual up to 6 individuals per sq. mm. Some groups have individuals in contact with, or even attached to, one another, but the amount of crowding depends upon the species. Some are more solitary and others more gregarious, their habits in settling being part of their specific nature.

Thus \( M. \ andrewsi \) is most prone to present some clusters attached by common "coletoderm," or cement, and \( P. \ amphora \) most apt to appear as isolated individuals. Dons (11) gives a photograph of small clusters of his \( Parafolliculina \ roestensis \) which he supposes due to one original settler giving rise to offspring that settled down close to the ancestor; however, in \( M. \ andrewsi \) we have observed large aggregates made by the nearly simultaneous settling of many young that were influenced by one another in clumping together. Probably the secretions, issuing from each as it swims and settles, influence mechanically others that are drawn to the same region.

While most all the recorded occurrences of folliculinids were made in the summer season (the vacation of a naturalist) some of those on oysters are the winter exceptions, and this seems of import in such side branches of the Chesapeake as the Severn River where, in the months of July and August, vast swarms of folliculinids may be found on submerged vegetation along the shores, coming after the annual growth of the plants has started and disappearing mysteriously before it ceases. The question of where these species exist in the winter is partly answered by the finding of both of them on oyster shells in the nearby beds of Round Bay, Md.

Maps published by the U. S. Coast and Geodetic Survey (21) indicate four small oyster bars in Round Bay that may total an area of about one square kilometer, or roughly 1,196,551 square yards; and the estimates made by Caswell Grave (14) in 1912 define a bed as
profitably workable for tongers at depths of 22 feet if the oysters on the bottom are about an average of 15 to the square yard. Since some tongers use those beds, we infer they may find at least 15 to the yard, or there may be about 17,948,265 usable oysters over the bottom of Round Bay (about eighteen million).

From our few observations it would seem that folliculinids may occur on about 30 percent of these oysters, or approximately on 6 million oysters. Again the number of folliculinids to be expected on an average oyster here is very uncertain, but it might be about thirty; so we suppose that about 180 million folliculinids are resident on the oyster shells of the Round Bay bars.

When in midsummer the water is very warm and the plants in the shallow waters along the shore are well grown, the great numbers of folliculinids found on their leaves may have migrated from the oyster beds; if Round Bay beds do not supply sufficient numbers there are also some miles of beds down the river from Round Bay to Annapolis, estimated in 1912 as 25 bars on both sides of the river in water 6 to 18 feet in depth, 998 acres in all, of which 100 acres might be made to produce oysters.

The hypothesis that folliculinids migrate from winter quarters on oyster shells to midsummer sojourn on submerged plants along shore is in harmony with the following observations: while in the eastern part of Round Bay there were many folliculinids on the oysters in April, there were but few in June, and in the western part, though abundant in December and in March, none were found in July 1943, these observations being based on a pocket-lens examination of some hundreds of shells and a thorough examination of eighteen shells, secured by the Maryland Department of Tidewater Fisheries; yet at the same time some were seen on leaves of potamogeton along the nearest shore, as well as up Weems Creek.

In the summer season much migration of folliculinids from lower to upper parts of plants was inferred, yet there were some instances of increase in numbers and possibly some seasonal outbursts of multiplication which might be bound up with conjugation, about which nothing is yet known in the Folliculinidae.

The same hypothesis of migration, with or without multiplication, may be applied to other arms of the Chesapeake where folliculinids, in the absence of rocky shores, are found in warm weather attached to elodea and other aquatic flowering plants near the shores. Thus the folliculinids found far up Middle River might owe their origin to immigrants from such oyster beds as those off Tolchester Beach, which, standing at the limit of oyster beds toward the fresh waters
of the head of the Bay, are subject to destruction in freshets, yet supplied in 1910 many thousands of bushels of marketable oysters at the rate of 91 bushels to the acre.

It is to be emphasized that while folliculinids were very abundant up Middle River, at Clark's Point in 1941, none could be found in 1942 at an earlier period of the summer; apparently, while conditions were favorable, the folliculinids had not yet arrived. While present in late November 1941, with water temperature 9° C and pH 7.8, they were not present late May to late July 1942, with water at 20-27° C and pH 8.7-8.3. One year they had been brought there by favorable winds and currents, but next year they had not yet been able to migrate there? Folliculinids are known to feed on bacteria, as well as on diatoms and some minute algae, but the conditions that favor a flourishing community are not known sufficiently to make successful attempts to culture these protozoans in the laboratory.

From an enumeration of the localities in which each of ten known species in North America are found, it appears that five of them may occur on oyster shells, one as a hypercommensal on the egg capsules of turbellarian worms attached to the gill plates of the arachnoid Limulus, two on the posterior part of the abdomen of hermit crabs, and one on the spiral calcareous dwelling of an annelid. But few sorts are restricted in choice of substrata.

On the hind end of hermit crabs within some snail shells conditions for existence are peculiar, but apparently favorable, as the folliculinids thrive there. Refuse accumulates in the inner end of the snail shell and it may be that bacteria found there aid in the food supply to the folliculinid. Possibly in a similar way the life on the shells of oysters may be profitable to folliculinids since they find an easy food supply of both bacteria and diatoms. Martin (17) and Nelson (19) advance the view that the diatoms and other organisms living in the community upon the oyster shell may serve as food for the oyster, growing there as in a garden to the profit of the oyster. They even suggest that some of the wastage from the oyster going back onto the shell serves to fertilize the crops in the garden. Martin (17) states: "Thus the oyster not only plants a garden upon its shell but fertilizes it."

Folliculinids have their enemies. Various aquatic insects and isopods mow off the tests and make use of them in constructing their own mucous dwellings. But one great drawback to the flourishing of folliculinids is the plugging of their tests with bacterial jelly and burial under accumulations of ooze and sediments. They also may be injured by such unusual parasites as Pottsia infusorium Chatton and Lwoff (8) which we observed attacking both M. andrewsi and P.
amphora from locations north of Baltimore off "Miami Beach", as well as *Platyfolliculina paguri* attached to the abdomen of the hermit crab, *Pagurus pubescens* (3) from Maine.

Some of the empty tests showed that the death of the animal resulted from attack by too many of these parasites. But empty tests arise constantly from the habit of the animal to abandon its test and swim free, in a reduced or larval form. Such free swimmers may add greatly to the plankton. In the Severn R. we took them to the number of 14–100 in a random quart of water (1). A possible utility for human beings may be found in these free swimming folliculinids, for their protoplasm, myonemes and nuclear material all should be good food for whatever animal could sieve them out of the innumerable quarts of water. In the late summer, schools of small young menhaden gyrate through the surface waters with open mouths that take in all sorts of plankton then present, and it is probable that they catch the folliculinids. Thus it may be the menhaden in part that account for the rapid disappearance of folliculinids along the shores of the Chesapeake branches. Eventually it may be proved that the menhaden digest these swimming folliculinids, and that would make the protozoan valuable as contributing to the profit man draws from menhaden fisheries. Again, some of the free swimmers starting from oyster shells might be taken in by oysters and possibly they may contribute to the oyster's food supply, which should endear them to man.

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